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Environmental heterogeneity causes differences in the amphibian assemblage structure of an undisturbed montane cloud forest in southern Mexico

[1,2]Carlos Omar Becerra-Soria, [3]Eduardo Pineda, [2]Gabriela Parra-Olea, and [2*]Omar Hernández-Ordoñez

[1]*Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Ciudad de México, MÉXICO* [2]*Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, MÉXICO* [3]*Red de Biología y Conservación de Vertebrados, Instituto de Ecología, A.C., Xalapa, Veracruz, MÉXICO*

Abstract.*—Mountain cloud forests (MCF) are one of the most diverse ecosystems due to their natural environmental heterogeneity and distribution. This ecosystem exhibits a high beta diversity at regional or local levels. In this study, the amphibian species diversity and assemblage structure were examined in a mountain cloud forest at El Triunfo Biosphere Reserve (ETBR) in southeastern Mexico. Ninety-six plots were sampled in eight sites, distributed in two core zones of protected mountain cloud forest. The amphibian species diversity, assemblage structure, and functional groups were analyzed and compared between the two zones; the relationships between environmental variables and amphibian diversity and the conservation status of the species were also examined. Based on six surveys conducted at each core zone over 24 months (1,536 person-hours), 306 individuals of 14 amphibian species were recorded, with only six species present in both core zones. While differences were found in the number of individuals and assemblage structure between the core zones, there were no differences in the number of species or the common or dominant species. *Craugastor matudai* was the most dominant species in both zones, while partial differences were found in the second- and third-most dominant species. While this study shows that the amphibian species diversity did not change within the extensive and conserved cloud forest of the ETBR, slight variations were observed in the structure of the amphibian assemblages and composition of species. The environmental heterogeneity (mainly humidity, temperature, and canopy cover) of the mountain cloud forest seems to determine the variation in the species assemblages between the different zones and the areas that make up this ecosystem. Nine amphibian species (64%) found in the ETBR are under an IUCN threat category. This study is one of the few that addresses the structure of amphibian assemblages in a large, well-preserved mountain cloud forest.

Keywords. El Triunfo, biosphere reserve, amphibians, communities, environment, microhabitat, canopy

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Introduction

The montane cloud forests (MCFs) are characterized by cloudy, wet, and difficult terrain, and are generally located at the mid-elevations of tropical mountain systems (Bruijnzeel et al. 2011; Scatena et al. 2011). MCFs are among the most biodiverse ecosystems worldwide and are characterized by high levels of endemism (Karger et al. 2021; Williams-Linera 1994, 1997). However, it is also one of the most threatened tropical ecosystems globally (Aldrich et al. 1998; Gentry 1995; Hamilton et al. 1995; Karger et al. 2021).

In Mexico, the MCF is represented by small and discontinuous remnants, occupying less than 1% of the national territory, of which only 12% are protected (Ponce-Reyes et al. 2012; Rzedowski 1996). Nevertheless, Mexican MCFs are considered the most diverse per unit area, containing 10% of the native flora (Rzedowski 1998) and 12% of the terrestrial vertebrates

Correspondence. **omar.hernandez@ib.unam.mx*

(Flores-Villela and Gerez 1994) in Mexico. Due to the high environmental heterogeneity and singular biogeographic history (Campbell 1999; Challenger 1998; Churchill et al. 1995; Rzedowski 1998, 2006), the MCF ecosystem exhibits high beta diversity levels at regional (Jankowski et al. 2009) and local scales (i.e., in the same patch of the forest) (Ledo et al. 2009; Williams-Linera 2002). This pattern is especially true for taxa with low vagility and those sensitive to environmental changes such as amphibians (Díaz-García et al. 2017; Hilman et al. 2014; Wake and Vredenburg 2008).

The El Triunfo Biosphere Reserve (ETBR) was decreed a protected natural area 31 years ago, and the process of investigating its total biodiversity is still in progress. The ETBR is a protected natural area located in the central part of the Sierra Madre de Chiapas physiographic region in Chiapas, in southern Mexico. It covers an area of approximately 119,177 ha and contains seven of the ten vegetation types identified for Mexico by Rzedowski (2006). Of the total area, 78% (93,458 ha) corresponds to the buffer zone, including 43 ejidos (land farmed communally), 162 privately owned lands, and one town. The remaining 22% (25,718 ha) is composed of federal lands distributed in five polygons or core zones: El Triunfo, Ovando, El Quetzal, El Venado, and La Angostura (Carabias-Lilo 1998; Enríquez 2019). Notably, the ETBR has the most extensive, continuous remnant of protected MCF in Mexico (Lopez-Arce et al. 2019; Ponce-Reyes et al. 2012), and is considered the most diverse MCF in the country (Lopez-Arce et al. 2019; Pérez-Farrera 2004). Regarding amphibians, the few studies performed in the ETBR reported dissimilar figures of total species richness. Espinoza et al. (1999) recorded 18 species of amphibians, while Muñoz-Alonso et al. (2000) reported a total richness of 25 species which increased to 29 species in a subsequent survey (Muñoz-Alonso et al. 2004). Reynoso et al. (2011) reviewed all the lists and agreed with the total proposed by Muñoz-Alonso et al. (2000).

In this study, two of the five core zones of the mountain cloud forest were sampled. The Triunfo Core Zone (TCZ) is the largest and most studied, with the easiest access and the best infrastructure. The TCZ is also the most turistic and the most protected core zone in the reserve. The Quetzal Core Zone (QCZ) is the smallest core zone and the closest to the TCZ. Both zones have large areas of MCF and are considered to represent the same ecosystem (Rzedowski 2006). Given the intrinsic environmental heterogeneity of mountain cloud forests in general, one would expect this heterogeneity to translate into differences in the characteristics of amphibian communities that inhabit the forest, such as species diversity, assemblage structure and composition, and their functional groups. In this sense, the characteristics of the cloud forest in ETBR (since it is well-conserved and extensive) represent a great opportunity to study the relevance of the environmental heterogeneity of a cloud forest on amphibian communities.

Therefore, this study aims to understand the role of the environmental heterogeneity within a well-preserved and extensive cloud forest on the diversity and structure of the amphibian species assemblages. This assessment consists of five components: (1) examine and compare the amphibian species diversity and abundance between two core zones of undisturbed old-forests within the ETBR, (2) analyze the structure of species assemblages, (3) determine and compare the functional groups that inhabit the two core zones, (4) examine the influences of key environmental variables on the amphibian species diversity, and (5) review the conservation status of the species recorded in this study. This study is the first in Mexico, and perhaps in Mesoamerica, that evaluates and describes the amphibian assemblage in a large and well-preserved mountain cloud forest.

Methods

Study area. The study was conducted in two core zones of a well-preserved MCF, El Triunfo (TCZ) and El Quetzal (QCZ), within the ETBR (15°09'–15°57'N, 92°34'–93°12'W). The TCZ and QCZ are neighboring core zones with similar altitudes, but they have different sizes and topographies (Fig. 1). The TCZ is the largest core zone in the ETBR at 11,595 ha. Its MCF is located topographically between 1,900 and 2,100 m asl, in the form of a platform. Its annual precipitation is approximately 3,044 mm, and the average annual temperature is 20 °C (Martínez-Camilo et al. 2012). The QCZ is the smallest core zone, covering 1,193 ha, with an altitudinal range between 1,200 and 2,500 m asl. Its MCF is located between 1,850 and 2,250 m asl. The topography is mainly mountain peaks with steep slopes. The annual precipitation is approximately 2,152 mm, and the average annual temperature is 21.2 °C (Martínez-Meléndez et al. 2008).

Sampling protocol. Between 2014 and 2016, a total of six field trips were conducted in three different seasons (two samplings per season): Dry (February–May), Warm-wet (June–September), and Cold–wet (October–December). To represent the local environmental heterogeneity in each core zone, four sites separated by at least 500 m were selected. Within each site, 12 plots (50×50 m^2) were established, for a total of 48 plots per core zone (Fig. 1).

To include the peak hours of diurnal and nocturnal activity (Jones 1986), each plot was sampled by four people for two hours during the day (1100 to 1300 h) and two hours during the night (2100 to 2300 h). Thus, the sampling effort represented a total of 768 person/h per core zone. Specimens were identified to species using standard field guides (Campbell 1998; Kohler 2011; Lee 1996).

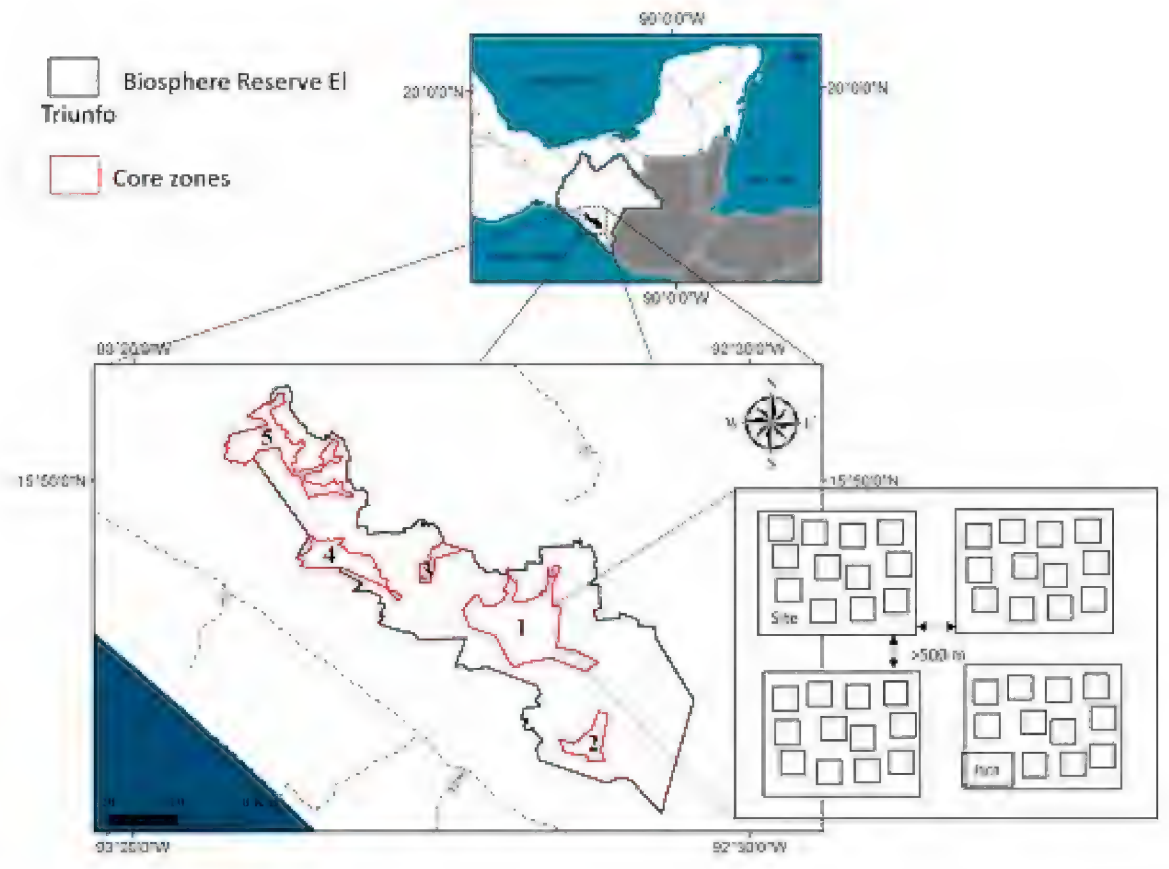

Fig. 1. Location of the two sampled zones, El Triunfo core zone [TCZ] (1) and the El Quetzal core zone [QCZ] (3), in the El Triunfo Biosphere Reserve (ETBR), Sierra Madre de Chiapas, Mexico, and illustration of the sample design (core zones, sites, and plots).

Two complementary sampling methods were used to adequately cover the sample areas (Ribeiro-Júnior et al. 2008). First, amphibians were collected from all possible microhabitats during direct searches (visual and auditory) using a time-constrained technique (Crump and Scott 1994). The second method was canopy sampling of two trees in each plot with characteristics that enable the presence of amphibians (i.e., presence of bromeliads, moss, and tree holes) (Vonesh et al. 2009). The selected trees had a height of at least 20 m and a diameter at breast height larger than 3 m. The canopy was sampled using the single rope technique (Perry 1978; Perry and Williams 1981), which consisted of the assurance of a static rope, in different branches. All potential microhabitats in the trees were searched by four people, two in the understory and two in the canopy, in each plot. To minimize disturbance to the microhabitats, all surface cover objects were returned to their original position (Vonesh et al. 2009).

Functional groups. To establish functional groups within the two core zones, we selected seven functional traits (body size, toe webbing, mouth width, leg length, dorsum skin thickness/type, respiration type, and fecundation type) and eight life-history traits (male reproductive display for female response, male reproductive display site, fecundation site, egg-laying site, parental care of clutches, daily activity, habitat during non-breeding season, and the number of habitats used in non-breeding season). These morphological and physiological characteristics were measured at individual levels without reference to the environment or any other level of organization, and they are related to individual growth, reproduction, and species survival (Duellman and Trueb 1994; Wells 2007). Additionally, they explain amphibian functions within the ecosystem (Cortés-Gómez et al. 2015). Trait categories were established based on the published literature (AmphibiaWeb 2021; Duellman 2013; Raffaelli 2014), complemented with data from our field surveys (Supplemental Table 1). To identify functional groups (FG) between species, a functional dendrogram was constructed based on a species trait matrix using Euclidean distance and unweighted pair-group arithmetic average clustering (Bihn et al. 2010). The statistical significance of the observed FG between amphibian species was assessed with a Euclidean distance matrix and a similarity test (ANOSIM; 999 permutations).

Environmental conditions. Five environmental variables for each plot (temperature, humidity, elevation, canopy cover, and distance to the closest stream or pond) and five variables where the individuals were observed (temperature, humidity, percentages of substrate [leaf litter, rock, or herbaceous], leaf litter depth, and understory cover) were quantified (Urbina-Cardona et al. 2006). The elevation was measured with an altimeter (Garmin Etrex 30) by averaging the values obtained from three randomly chosen places on the plot. The canopy cover was obtained by analyzing three pictures in each plot: one in the center, and two in the opposite vertices of the plot. The pictures were taken on high luminosity days with a 180° hemispherical

lens at a height of 1.5 m. The percentage of canopy cover was calculated with the software Gap Light Analyzer (Frazer et al. 1999). The presence of streams and ponds or the distance from the nearest water body were measured from the center of each plot. The temperature and relative humidity were measured at three points in the plot with three HOBO U23 Pro v2 data loggers (Onset, Bourne, Massachusetts, USA) during the entire sampling day. The temperature and humidity were recorded with a thermo-hygrometer after 20 s of exposure. The leaf litter depth was measured by introducing a graduated ruler into the litter on the soil. The relative understory density was obtained by averaging the number of contacts of the vegetation (branches, stumps, and leaves) with a pole (3.5 cm in diameter and 1.5 m in height) placed vertically at five random points in the plot (Urbina-Cardona and Londoño 2003; Urbina-Cardona et al. 2006). Finally, the substrate components of herbaceous, leaf litter, and soil cover were estimated using a 0.3 × 0.3 m quadrant divided into four quadrants with a nylon string (Urbina-Cardona et al. 2006) (Supplemental Table 2).

Data analyses. To ensure that species diversity was adequately assessed at each site and to ensure valid comparisons of Hill's Numbers (see below) between core zones, the Sample Coverage Estimator was calculated for each core zone (Chao and Jost 2012; Pineda and Moreno 2015) using iNext software (Hsieh et al. 2016). This coverage estimator is sensitive to species with one (singletons) or two (doubletons) individuals (Chao and Jost 2012). For each site, ecological diversity was measured with Hill's Numbers (Chao et al. 2006, 2014; Tuomisto 2010), which show the effective number of species, and are useful for assessing patterns of species diversity by giving different weights to species relative abundances (Chao et al. 2006, 2014). In particular, we considered Hill's Numbers of order 0 (^{0}D, species richness), order 1 (^{1}D, Exponential Shannon Entropy), and order 2 (^{2}D, Inverse Simpson). ^{0}D is not sensitive to species relative abundance, giving the same weight to all species, and denotes the number of species. ^{1}D is interpreted as the number of common species within the community. ^{2}D indicates dominant species and is therefore interpreted as the number of very abundant species within the community (Chao et al. 2006). For the three diversity metrics, the SpadeR Software was used to randomize 100 times. To compare the ^{1}D and ^{2}D, we extrapolated the abundance to the double number of individuals from the core zones with the lowest number (Chao and Elsensohn 2010; Chao and Jost 2015; Colwell et al. 2012; Hsieh et al. 2016). Generalized Linear Models (GLM) were used to assess differences in the community attributes between the two core zones, with a fixed Gaussian Error Distribution for ^{0}D, ^{1}D, and ^{2}D. In case of counting data (^{0}D and number of individuals), a Poisson and Quasipoisson error distribution was fixed.

Differences in the assemblage structure were assessed by constructing Species-rank Curves (SRCs) for each core zone. The relative abundance of each species (*PAi*) was plotted on a logarithmic scale against the Species Rank (*SRi*, species ordered from the most to the least abundant; Magurran 2004). The slope of the SRC represents the evenness in abundance among species within an assemblage.

Multidimensional Scaling (MDS) based on a Chao Distance Matrix was used to examine the overall dissimilarity of the amphibian community structures between the two core zones. MDS was completed using the Function Meta MDS in the Vegan package for version R 1.3 (R Core Development Team 2004). Using this matrix, a Non-parametric Two-way Analysis of Similarity (ANOSIM) was performed to test the hypotheses regarding the spatial differences in the amphibian composition. The ANOSIM procedure is a permutation-based test that can be applied to simple nested designs (e.g., core zones within natural protected areas) to detect differences between groups (Clarke and Gorley 2001).

To determine the relationships between various environmental factors and species distribution, a Pearson Coefficient was used to identify all non-correlated variables. All 10 measured variables achieved normality and homoscedasticity of variance. With the remaining variables from the Pearson Correlation Coefficient, a Canonical Correspondence Analysis (CCA) was used to detect the relationships between species distribution and microhabitat variable responses to environmental gradients (Urbina-Cardona et al. 2006). In CCA, statistical significance indicates that the observed associations between species and environmental variables are not random (Ter Braak 1987; Kent and Coker 1992).

To identify differences in environmental conditions between the two core zones, Generalized Linear Models (GLM) were used with fixed Quasibinomial Error Distribution canopy cover and soil cover (percentage) and Gaussian Error Distribution for data with a normal distribution. Principal Component Analysis (PCA) was also performed using the environmental variable averages of the 12 plots per site (e.g., distance from the nearest water body, canopy cover, understory density, plot temperature, and humidity).

Finally, to assess the effect of environmental variables on assemblage structure, a Mantel test was performed (Sokal and Rohlf 1994). The environmental matrix was based on the first two axes of the PCA (per site), and the amphibian Assemblage Structure Matrix was based on the relative abundance of species per site. The Mantel test was performed with the R-package statistical software (Legendre and Vaudor 1991), and significance was assessed using a Monte-Carlo procedure with 999 permutations (Mantel test, $p<0.05$, 999 permutations).

For CCA, PCA, and Mantel tests, the Vegan package of R software was used (Oksanen et al. 2016).

Results

Species diversity and abundance. The surveys of the 96 plots yielded a total of 306 amphibian individuals, representing 14 species—10 frogs and four salamanders (Table 1). The QCZ had the highest numbers, with 194 individuals belonging to nine species (three salamander and six anuran species), while the TCZ surveys yielded 112 individuals representing 11 species (three salamander and eight anuran species). Of the 14 amphibian species, only six were present in both core zones, whereas five were exclusive for the TCZ and three for the QCZ.

The sample coverage values for TCZ and QCZ were 0.96 (±0.03 IC 95%) and 0.99 (±0.01 IC 95%), respectively. The QCZ had almost twice as many individuals as TCZ (194 vs. 112, Fig. 2a). Although all the taxonomic diversity metrics (number of species, number of common species, and number of dominant species) were higher in TCZ than QCZ, the GLM did not present statistical differences between the two core zones (Fig. 2b–d).

Assemblage structure. *Craugastor matudai* was the dominant species in both core zones (52 individuals in TCZ and 64 in QCZ), the second and third most dominant species in the QCZ were the salamander *Bolitoglossa occidentalis* (49 individuals and not detected in TCZ), and the treefrog *Plectrohyla matudai* (47 individuals); while, *Bolitoglossa franklini* (37 individuals) was the second most dominant species in the TCZ. The TCZ had five species with a single individual: *Bolitoglossa flavimembris, Dendrotriton xolocalcae, Exerodonta sumichrasti, Duellmanohyla schmidtorum,* and *Plectrohyla lacertosa*, while the QCZ had only one (*Lithobates maculatus*) (Fig. 3a).

Nonmetric Multidimensional Scaling closely grouped the TCZ sites in MDS axis-1, which means that the community structure and species composition did not vary between sites, while QCZ sites were over dispersed along the two axes (Fig. 3b). It should be noted that along

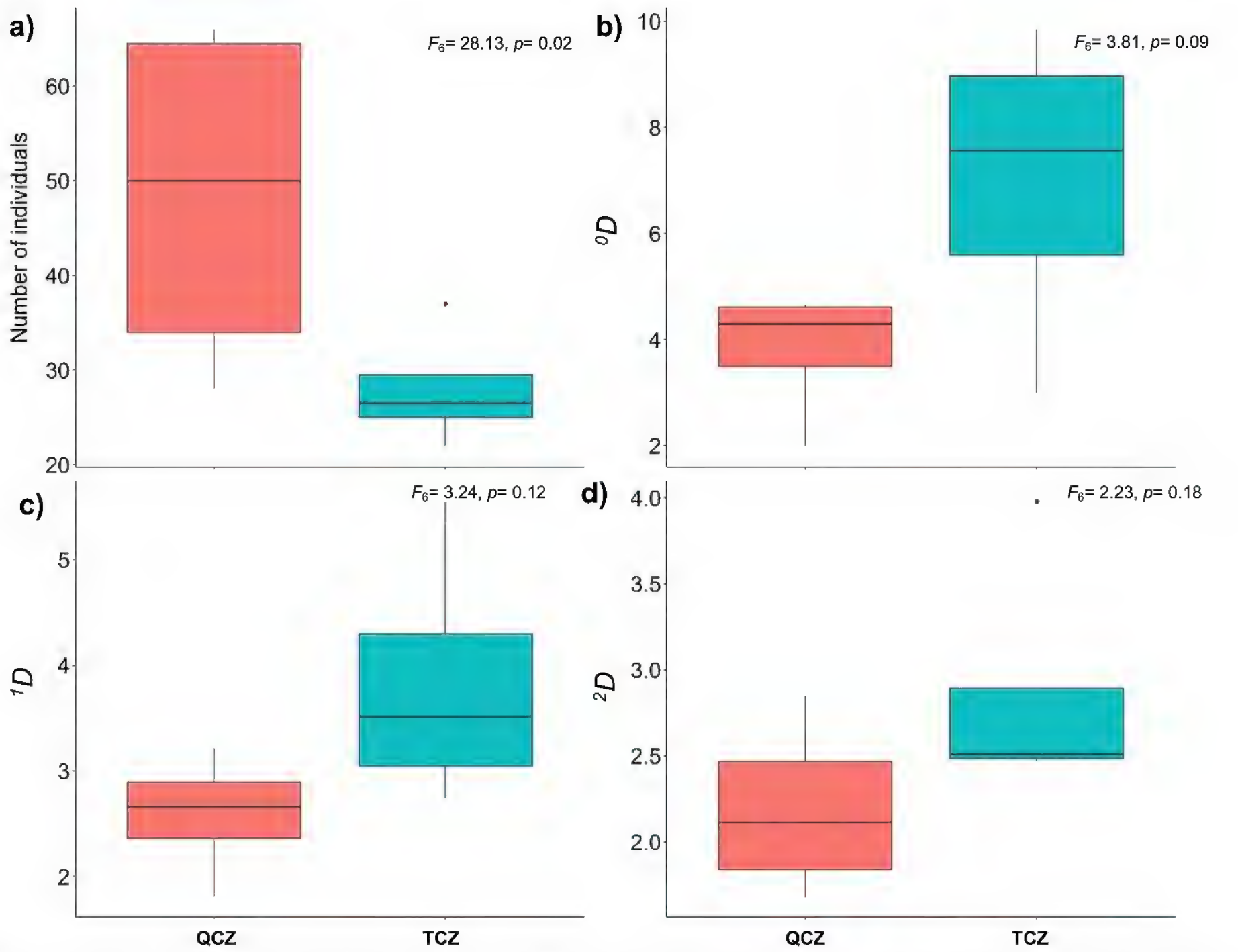

Fig. 2. Box plots of amphibian species diversity in the El Triunfo Biosphere Reserve (ETBR), Chiapas, Mexico, showing the median (solid line), 25th and 75th percentiles (boundaries of boxes), and minimum and maximum (lines). (**a**) Number of individuals, (**b**) Species richness (^{0}D), (**c**) Common species (^{1}D), and (**d**) Dominant species (^{2}D).

MDS axis-1, one QCZ site (QCZ-1) was closer to the TCZ sites than to the remaining QCZ sites, resulting in no statistical differences (ANOSIM) between the core zones. Notably, the QCZ-1 site was the only one where *Bolitoglossa franklini* was recorded (Table 1).

Functional groups. According to the Euclidean distances, the functional dendrogram presented five functional groups (Fig. 3c), and the similarity test (ANOSIM) indicated significant differences among the groups (*R*statistic = 0.99). The 14 species were grouped in relation to the values of the traits shown in the Principal Component Analysis, which explained 73% of the variance (Pc1 48.08% and Pc2 25.12%, Supplemental Fig. 1). Five groups were present in the QCZ, while the TCZ had only four groups. Anurans and salamanders (all plethodontids) were separated by mouth width and respiration type. The first anuran group (FG1) included only the frog *L. maculatus,* which was grouped by the leg length trait; the second group (FG2) included the craugastorid frogs (*C. matudai* and *C. stuarti*), which were grouped by parental care; and the third group (FG3) included seven hylid species (*Pl. matudai, Pl. hartwegi, Pl. lacertosa, Pl. sagorum, D. schmidtorum, E. sumichrasti,* and *Pt. euthysanota*), which were grouped by laying site and leg length traits. The fourth and fifth groups included the Plethodontidae species, which were grouped by respiration type. The fourth group (FG4) included only the salamander *D. xolocalcae*, which was grouped by its arboreal habit trait. Finally, the fifth group (FG5) included three *Bolitoglossa* species (*B. occidentalis*, *B. franklini*, and *B. flavimembris*), which were grouped by the male reproductive display and fertilization site traits.

Relationships between environmental conditions and amphibian species. In the PCA, the two main axes explained 78% of the total environmental variation. PCA axis-1 explained 48%, and axis-2 explained 30% (Fig. 4a). The four sites in the TCZ presented higher environmental similarity related to conditions of higher humidity and canopy cover. In contrast, the four sites in the QCZ presented higher environmental heterogeneity.

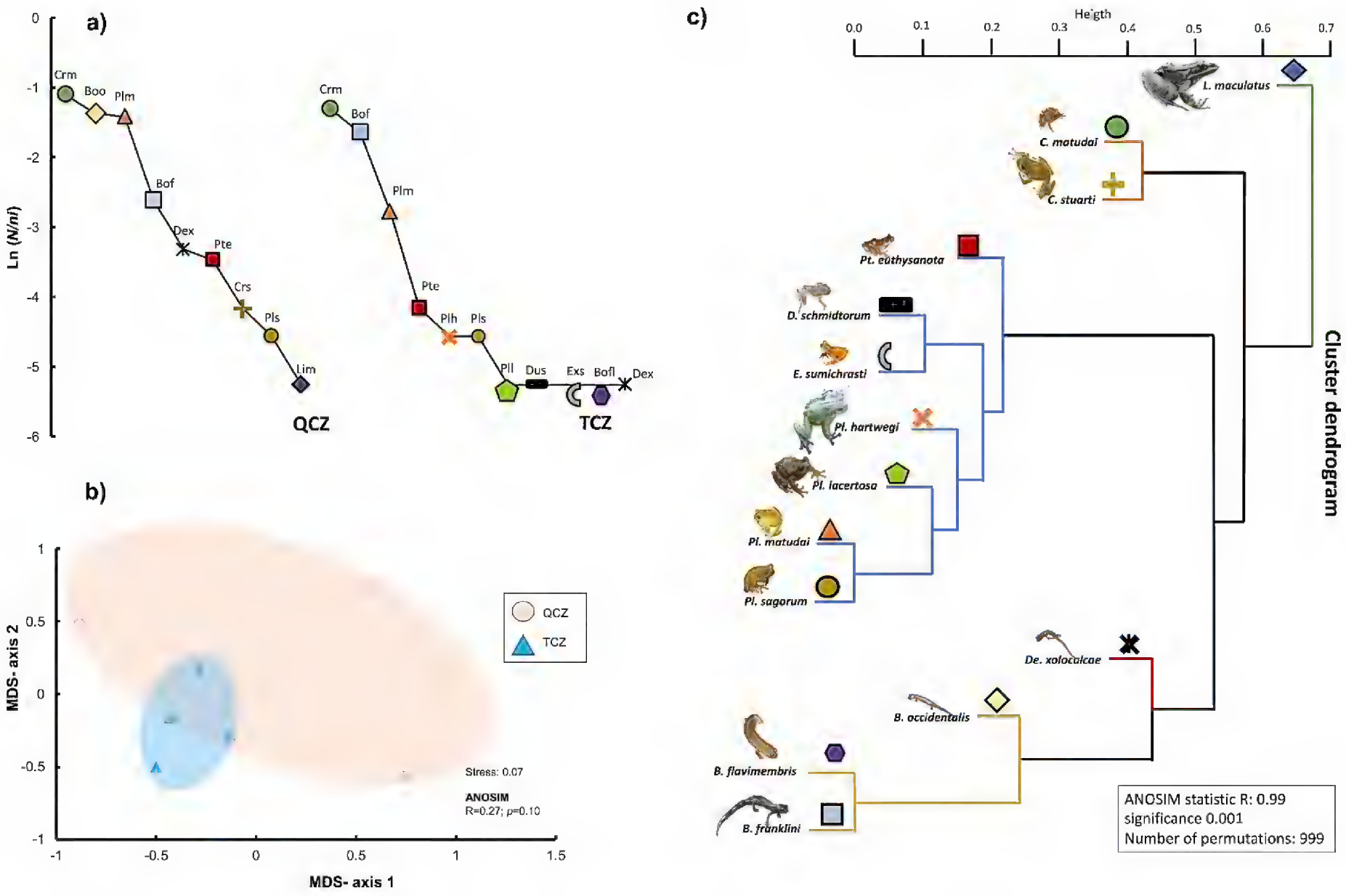

Fig. 3. (**a**) Rank-abundance Curves for the El Triunfo core zone [TCZ] and Quetzal core zone [QCZ] in the El Triunfo Biosphere Reserve. Letters on the Rank-abundance Curves correspond to Crm (*C. matudai*), Crs (*C. stuarti*), Pll (*Pl. lacertosa*), Plh (*Pl. hartwegii*), Plm (*Pl. matudai*), Pls (*Pl. sagorum*), Dus (*D. schmidtorum*), Pte (*Pt. euthysanota*), Exs (*E. sumichrasti*), Lim (*L. maculatus*), Bof (*B. franklini*), Boo (*B. occidentalis*), Bofl (*B. flavimembris*), and Dex (*D. xolocalcae*). (**b**) Nonmetric multidimensional scaling of the eight sites within the core zones in the ETBR. Blue triangles: TCZ sites, pink circles: QCZ sites. (**c**) Dendrogram of functional groups of the El Triunfo core zone amphibian species, using Euclidian Distance, and tested functional groups by ANOSIM are highlighted in different colors (FG1: green; FG2: brown; FG3: blue; FG4: red, and FG5: yellow).

Table 1. Amphibian species recorded in two core zones, number of individuals per site, and IUCN and NOM-059 categories in El Triunfo Biosphere Reserve, Mexico. Letters in the Code column are species codes for the Rank-abundance curves shown in Fig. 3.

Species	Code	Quetzal core zone					El Triunfo core zone					IUCN	NOM-059
		QCZ-1	QCZ-2	QCZ-3	QCZ-4	QCZ total	TCZ-1	TCZ-2	TCZ-3	TCZ-4	TCZ total		
ANURA													
Craugastoridae													
Craugastor matudai	Crm	6	9	23	26	64	22	9	6	15	52	Endangered	Special protection
Craugastor stuarti	Crs	0	0	3	0	3	0	0	0	0	0	Vulnerable	Special protection
Hylidae													
Plectrohyla lacertosa	Pll	0	0	0	0	0	0	0	1	0	1	Endangered	Special protection
Plectrohyla hartwegi	Plh	0	0	0	0	0	0	1	1	0	2	Endangered	Special protection
Plectrohyla matudai	Plm	0	45	3	0	48	2	1	3	5	11	Least Concern	Not evaluated
Plectrohyla sagorum	Pls	1	0	1	0	2	1	1	0	0	2	Vulnerable	Not evaluated
Duellmanohyla schmidtorum	Dus	0	0	0	0	0	0	0	1	0	1	Near Threatened	Special protection
Ptychohyla euthysanota	Pte	0	6	0	0	6	2	0	1	0	3	Least Concern	Threatened
Exerodonta sumichrasti	Exs	0	0	0	0	0	1	0	0	0	1	Least Concern	Not evaluated
Ranidae													
Lithobates maculatus	Lim	0	1	0	0	1	0	0	0	0	0	Least Concern	Not evaluated
CAUDATA													
Plethodontidae													
Bolitoglossa franklini	Bof	14	0	0	0	14	7	14	9	7	37	Vulnerable	Special protection
Bolitoglossa occidentalis	Boo	0	3	36	10	49	0	0	0	0	0	Least Concern	Special protection
Bolitoglossa flavimembris	Bofl	0	0	0	0	0	1	0	0	0	1	Endangered	Special protection
Dendrotriton xolocalcae	Dex	7	0	0	0	7	1	0	0	0	1	Vulnerable	Special protection
Total number of individuals		28	64	66	36	194	37	26	22	27	112		

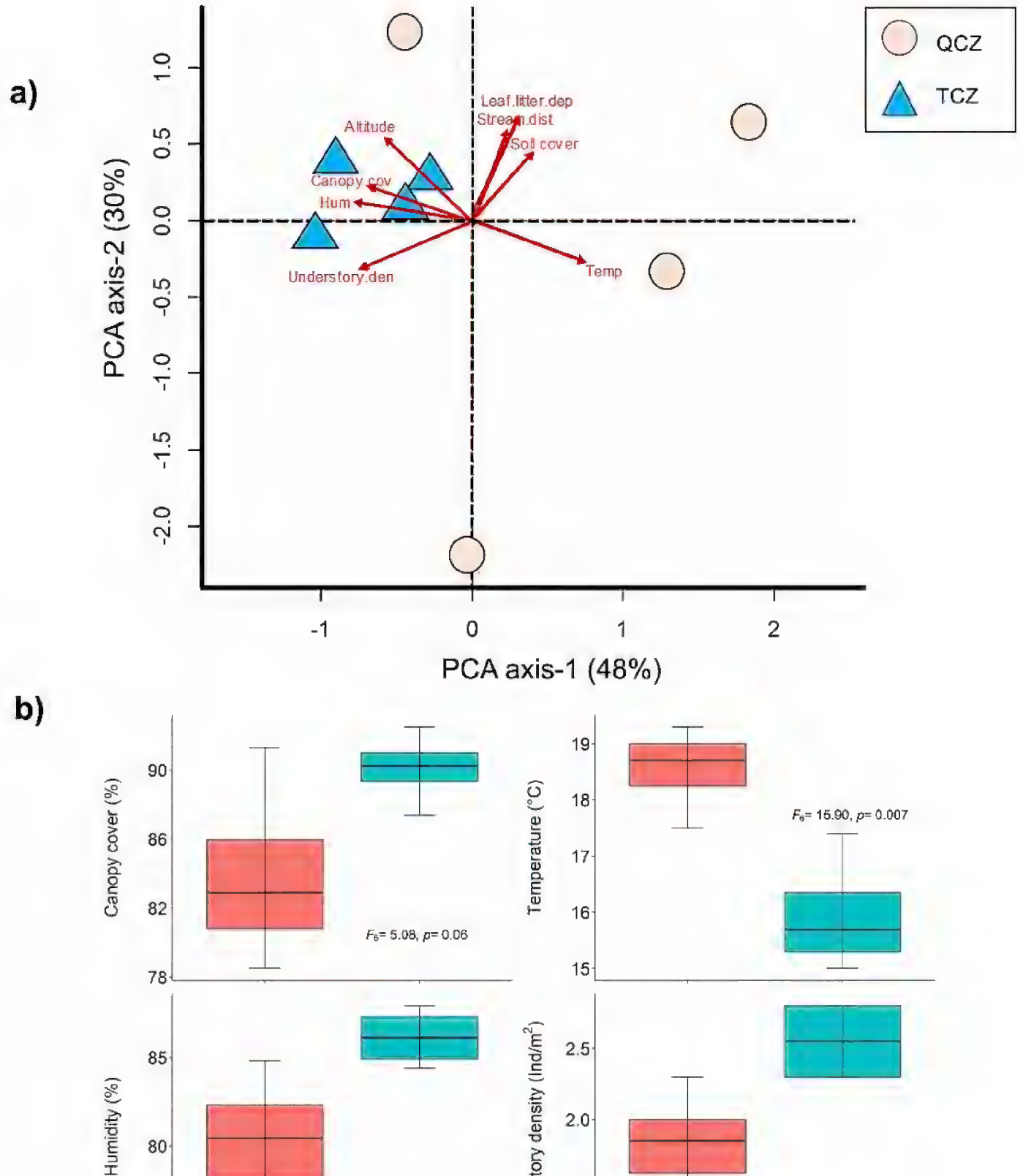

Fig. 4. (a) Principal Component Analysis, grouping the eight sites present in the core zones according to eight environmental variables taken in each site. Blue triangles: TCZ (El Triunfo core zone) sites; pink circles: QCZ (El Quetzal core zone) site. (b) Eight environmental variables measured in the eight sites (four per core zone). Median (solid line), 25th and 75th percentiles (boundaries of boxes), minimum and maximum (lines).

The Generalized Linear Models showed statistical differences in temperature, humidity, and elevation between the two core zones (Fig. 4b). The Mantel test showed a strong correlation between the differences in amphibian assemblage structure and the environmental conditions ($r = 0.73$, $p = 0.008$).

The Pearson Correlation Analysis showed that understory cover + humidity (plot) and soil coverage + leaf litter depth presented a high correlation (Table 2). In the CCA using the number of individuals per species, 83.64% of the variation in amphibian assemblages attributed among the core zones could be explained by environmental factors (CC-axis1 explained 44.90% and CCA-axis2 explained 38.74%).

The distribution of species was positively grouped based on the environmental variables (Fig. 5). *Bolitoglossa occidentalis* was correlated with higher average temperatures (20.8 °C). In contrast, *B. franklini, D. xolocalcae,* and *Pl. sagorum* were correlated with lower average temperatures (15.94 °C, 16.25 °C, and 16.26 °C, respectively), and higher humidity. *Plectrohyla matudai* and *Pt. euthysanota* were correlated with a microhabitat of higher understory density. Finally, *C. matudai* was correlated with deeper leaf litter depth and more leaf litter cover.

Threatened Species Inhabiting the El Triunfo Biosphere Reserve

Of the 14 species recorded, four (29%) are in the Endangered category of the IUCN Red List (*C. matudai, Pl. hartwegi, Pl. lacertosa,* and *B. flavimembris*); four (29%) are in the Vulnerable category (*B. franklini, D. xolocalcae, C. stuarti,* and *Pl. sagorum*); one (7%) is in the Near Threatened category (*D. schmidtorum*); and five (35%) are of Least Concern (*Pl. matudai, E. sumichrasti, L. maculatus, Pt. euthysanota* and *B. occidentalis*) (IUCN 2019).

In agreement with the Mexican government threatened species list (SEMARNAT 2010), *Pt. euthysanota* is the only species in the Threatened category (7%); while nine (64%) are under the Special Protection category (*C. matudai, C. stuarti*, *D. schmidtorum, Pl. lacertosa, Pl. hartwegi, B. franklini, B. flavimembris, B. occidentalis,* and *D. xolocalcae*); and finally, 29% of the species have not been evaluted by NOM 059. (*Pl. sagorum, Pl. matudai, E. sumichrasti,* and *L. maculatus*) (SEMARNAT 2010).

Discussion

Although mountain cloud forests are among the most threatened tropical ecosystems in the world (Aldrich et al. 1998; Hamilton et al. 1995), there has been little work addressing the structure of amphibian assemblages in well-preserved mountain cloud forests (Diaz-Garcia et al. 2017, 2020; Pineda et al. 2005). This study shows that within an extensive and well-conserved cloud forest like the ETBR, the amphibian species diversity presented only slight variations in the structure of the amphibian assemblages and composition of the species. The environmental heterogeneity (mainly humidity, temperature, and canopy cover) of the mountain cloud forest seems to determine the variations in the assemblages of species between the different zones or areas that make up this ecosystem.

Both core zones within ETBR have similar levels of conservation, indicating that the environmental differences between the eight sites within the core zones are caused by natural processes, and not by human activities (Fig. 5b). Differences in the relative abundance of species and composition between the two core zones (Figs. 3, 4) suggest that the environmental conditions in an MCF with a wide extent influence only some of the species in the assemblage, but not all species. Those differences are indicated by the presence of such species

Table 2. Pearson Correlation Coefficients among the five environmental variables measured for each individual in El Triunfo, Chiapas, México.

	Temperature	Humidity	Understory density	Soil coverage	Leaf litter depth
Temperature	1.0000000	-0.6957944	-0.6442938	0.2538929	0.1504011
Humidity	-0.6957944	1.0000000	0.7270343	-0.3770742	-0.2755456
Understory density	-0.6442938	0.7270343	1.0000000	-0.5306524	-0.5912516
Soil coverage	0.2538929	-0.3770742	-0.5306524	1.0000000	0.6145746
Leaf litter depth	0.1504011	-0.2755456	-0.5912516	0.6145746	1.0000000

in only one of the core zones and in a notable variation of their relative abundance. Each core zone offers specific conditions created by the inherent heterogeneity of the MCF, which are differentially exploited by species or groups of species. The higher numbers of individuals of the dominant species in the QCZ (*Craugastor matudai, Bolitoglosa occidentalis*, and *Plectrohyla matudai*) can be explained by its topography (Figs. 4 and 5b). The steep slope in this core zone produces an environmental gradient, causing habitat heterogeneity which favors the presence of these species (Figs. 3b, 4a) (Kozak and Wiens 2010; McCain and Sanders 2010).

The differences in assemblage structure (i.e., dominant and rare species) that occur despite the short distance between the two core zones supports the hypothesis that the specific environmental characteristics of each core zone (Fig. 4) offer different resources and conditions that drive the presence and abundances of certain amphibian species in the ETBR. The QCZ has an altitudinal range from 1,600 to 2,500 m, and the site at higher altitudes presented colder temperatures and higher levels of moisture (QCZ_1; which is more similar to the TCZ sites), while sites at lower altitudes presented warmer conditions (QCZ_2, QCZ_3, QCZ_4) and had a greater amount of leaf litter, which can provide suitable habitat conditions and food resources for amphibians, particularly for the salamander *B. occidentalis* (Duellman 1999; Wake and Lynch 1976; Welsh and Droege 2001). These conditions resulted in differences in species abundance within the four sites and, therefore, a greater number of dominant species (Fig. 3). In addition, the TCZ sites presented similar environmental conditions, with lower temperatures, higher levels of moisture, and a greater number of bromeliads (Fig. 5b). These conditions favor the presence of the four TCZ-exclusive species of tree frogs (Duellman 1999; Naniwadekar and Vasudevan 2007) and the salamander *B. franklini*, which had higher individual numbers in the TCZ than in the QCZ (Wake and Lynch 1976). However, some studies have mentioned that other environmental characteristics not included in our surveys (i.e., vegetation structure and composition, fragment size, tree height, presence of prey and predators, epiphyte numbers, etc.) also influence the amphibian assemblage structure (Pineda and Halffter 2004; Murrieta-Galindo et al. 2014; Díaz-García et al. 2017).

The differences in the hierarchical positions of some species between the two sites are very remarkable (Fig. 3). For example, *B. occidentalis* was the second most abundant species in the QCZ, however, it was not detected in the TCZ. This salamander was recorded in three of the four QCZ sites; these sites are located at altitudes below 2,000 m asl (with higher temperatures) and have higher leaf litter depths (Fig. 5b). The highest altitudinal limit reported for this species is 2,000 m asl, and although this species is considered semi-arboreal (AmphibiaWeb 2021), most individuals in our surveys were recorded in leaf litter. Given that all individuals of *B. occidentalis* were found at night and none during daylight searches, we believe they might come down to the ground searching for food and return to their arboreal microhabitat during the day. *Bolitoglossa franklini*, the second most dominant species in the TCZ, is reported to be a semi-arboreal species but can also be found under bark or under logs, requiring pristine MCF habitat between 1,500 and 3,000 m asl (Raffaelli 2014). In our surveys, this species was found mainly in leaf litter or under logs in all TCZ sites, but only in one site (QCZ_1) in the QCZ. All of these sites are located at altitudes above 2,000 and maintain conditions with higher humidity, higher canopy covers, and lower temperatures (Fig. 5b).

The five functional groups observed were determined by associations of different traits, which indicates that our dendrogram represents a realistic representation of natural variation (Petchey and Gaston 2006). The respiration type was the principal trait dividing the 14 species into two main groups (cutaneous breathing and lung breathing). Among the anurans, the parental trait and skin type were the principal traits that divided the anuran species into three functional groups. Among Caudata, the principal trait was the habitat used during the non-breeding season (arboreal group and understory-leaf litter group). The 14 species were assembled according to their functional traits and environmental requirements. According to their functional needs, the craugastorids were observed in sites with a higher amount of leaf litter. The craugastorids are a diurnal group that can resist higher temperatures, and they need higher amounts of leaf litter as egg-laying sites (Duellman and Trueb 1994). These hylids were observed in sites near streams or ponds because most of their functional traits need humidity or a high density of understory, especially as they use these sites for mating vocalization or as egg-laying sites (Duellman 2013). The higher number of functional groups in the QCZ is due to the environmental heterogeneity present there. Species like *B. occidentalis* (higher temperature, leaf litter, and understory habitats), *D. xolocalcae* (higher humidity conditions and preference for bromeliads as microhabitat), and *B. franklini* (lower temperature and high humidity conditions) have opposing relations in their physiological and environmental requirements. On the other hand, the species present in the TCZ depend on environmental conditions such as humidity and understory density, which are important for egg-laying sites, especially in hylids.

Our surveys found 56% of the species previously recorded for the ETBR (Espinoza et al. 1999; Johnson et al. 2015; Muñoz-Alonso et al. 2000, 2004, 2013; Reynoso et al. 2011). However, several of the species not recorded in our sampling either occur at lower elevations (i.e., *Incilius canaliferus, Eleutherodactylus pipilans, E. rubrimaculatus, Leptodactylus fragilis*, *L. melanonotus*, *Lithobates forreri*, *Bolitoglossa flaviventris*, and *Dermophis mexicanus*) or are known to be common in

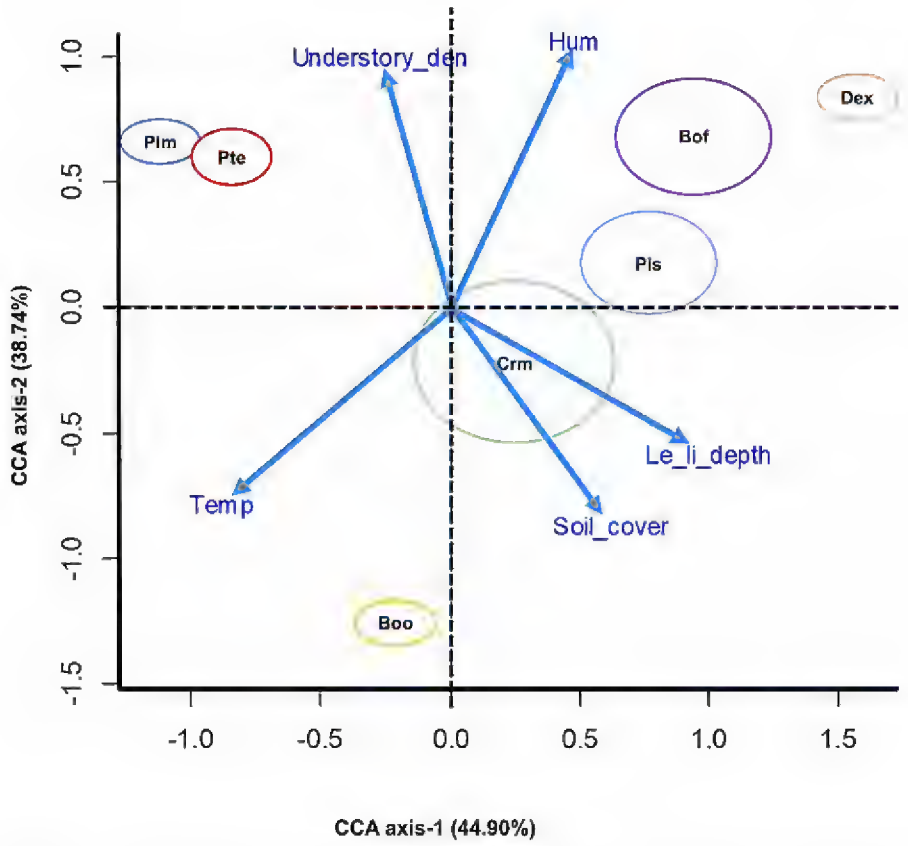

Fig. 5. Canonical Correspondence Analysis of the most common amphibians. The arrow orientation and length represent the association, direction, and strength between the environmental variables and the ordination axis. Species names correspond to: Crm (*C. matudai*), Plm (*Pl. matudai*), Pls (*Pl. sagorum*), Pte (*Pt. euthysanota*), Bof (*B. franklini*), Boo (*B. occidentalis*), and Dex (*D. xolocalcae*) Environmental acronyms correspond to: Hum (Humidity), Understory_Den (Under story density), Le_Li_depth (leaf litter depth), and Temp (temperature).

warmer more disturbed sites, such as *Incilius valliceps* and *Smilisca baudinii*. Interestingly, five species reported in the ETBR and not found in our sampling belong to the genus *Craugastor* (*C. greggi*, *C. lineatus*, *C. montanus*, *C. pygmeus*, and *C. rupinius*). Some of these species occur just in the boundaries of the reserve, such as *C. greggi*, *C. montanus*, and *C. lineatus*. On the other hand, this group of frogs is known to be difficult to identify morphologically, many of them have not been included in any molecular phylogeny, and their validity as species or placement within the genus remains uncertain (Padial et al. 2014).

This study contributes new information on how amphibian communities are strongly assembled by environmental variables. We observed changes in the composition and structure of amphibian communities either when comparing two core zones or even sites within the same core zone. Environmental variables such as temperature, humidity, depth of litter, and understory density were decisive for the assembly of amphibian communities since small changes in variables such as temperature and humidity can cause important changes in the diversity of the species, especially in the MCF. Furthermore, 70% of the amphibian species detected in our surveys are threatened species, which highlights their high conservation value, both as a whole and individually for each core zone. In this sense, to conserve the biota that inhabits an extensive cloud forest, it is necessary to protect the different zones or areas that comprise it, thereby capturing the forest's representative heterogeneity.

The amphibian assemblage in ETBR is composed of several species that are in an IUCN risk category (58% of species), and their relative abundances indicate the high levels of preservation that are needed in both core zones. For example, *Craugastor matudai*, an Endangered species, is the most abundant species for the two core zones; and despite the fact that the relative abundances of the other three Endangered species (*Pl. hartwegii*, *Pl. lacertosa*, and *B. flavimembris*) are not very high, they are still present in ETBR. Of the Vulnerable species (*B. franklini*, *D. xolocalcae*, *C. stuarti*, and *Pl. sagorum*), *C. stuarti* was registered only in the QCZ, and *D. xolocalcae* presented a higher number of individuals in the QCZ than in the TCZ. In contrast, the other three species were registered in both core zones with similar relative abundances.

Previous studies have reported evidence of local or even country-wide extirpation of some anurans, such as *P. hartwegi* (Lips 2004; Lips et al. 2004). Fortunately, we found two specimens of *P. hartwegi* in our surveys despite reports of it having been extirpated in Mexico (Santos-Barrera et al. 2004). The salamander *B. flavimembris* was reported for the first time in the TCZ and *D. xolocalcae* was reported for the first time in the QCZ. With these results, we emphasize that the ETBR is an important reserve for the maintenance of threatened species and both core zones are complementary in the maintenance of those species due to their environmental attributes.

In conclusion, the ETBR is a reserve of great extent that is in a good state of preservation. It is an ideal site for the study and protection of threatened organisms, such as amphibians. The ETBR has five core zones, with great environmental heterogeneity even between two adjacent core zones (TCZ and QCZ) which showed a direct effect in the distribution of the amphibian species. The other three core zones currently remain unstudied. In this study, we propose a combination of sample techniques (canopy, understory and leaf litter), to gain a better understanding of the community assemblage, and by using these techniques we were able to report the presence of very important frog and salamander taxa. The results of this survey can be used as a baseline for future studies regarding the amphibian community responses to the modification or loss of habitat, which is widespread in Mexico.

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Carlos Omar Becerra Soria is a Mexican Ph.D. student from Universidad Nacional Autónoma de México in Mexico. He began his study of amphibians in Dr. Parra's Lab in 2014. His research interests include cloud mountain amphibian communities, diversity, species conservation, vertical structure, and canopy diversity.

Eduardo Pineda is a titular researcher at the Instituto de Ecología, A.C. in Xalapa, Mexico. His research is focused on understanding the relationship between the transformation of tropical forest and biodiversity at different spatial scales, recognizing the importance of conserved areas and modified habitats to maintain amphibian diversity, and assessing (through fieldwork) the current situation of amphibian species in imminent danger of extinction. Currently he has several graduate students addressing topics in ecology and/or conservation of amphibians in Mexico and Latin America.

Omar Hernández Ordóñez is a collection manager at the National Collection of Amphibians and Reptiles at the Instituto de Biología, UNAM, Mexico. His research is focused on the conservation and community ecology of tropical rain forest herpetofauna, mainly evaluating the response of amphibian and reptile communities to habitat loss and modification.

Gabriela Parra Olea is a titular researcher at the Instituto de Biología, UNAM, Mexico. Her research is focused on the molecular systematics and conservation of Mexican amphibians. Her laboratory is formed by students and postdocs from different countries, such as Mexico, Guatemala, Costa Rica, Colombia, and Argentina, all working on research projects in systematics and taxonomy, conservation genetics, and the impact of infectious diseases, specifically chytridiomycosis, on the conservation of amphibians.

Supplementary Table 1. Sites, coordinates, environmental conditions, species registered, month, year, and season of sample for all 96 plots sampled in El Triunfo Biological Reserve. Species names correspond to a (*C. matudai*), b (*C. stuarti*), c (*Pl. lacertosa*), d (*Pl. hartwegii*), e (*Pl. matudai*), f (*Pl. sagorum*), g (*D. schmidtorum*), h (*Pt. euthysanota*), i (*E. sumichrasti*), j (*L. maculatus*), k (*B. franklini*), l (*B. occidentalis*), m (*B. flavimembris*), and n (*D. xolocalcae*).

Site			Coordinates	Altitude	Canopy cover	Distance to stream	Temperature	Humidity	Species	Month sample	Season
El Triunfo CZ	TCZ-1	Plot 1	15°39′21 N; 92°48′55	2,086	90	421	13.8	78	a, i, h	Feb 2014	Dry
		Plot 2	15°39′27 N; 92°48′51	2,055	92	248	17.6	88.6	a, k	May 2014	Warm-wet
		Plot 3	15°39′17 N; 92°48′56	2,100	80	513	12.3	83	a, h, k	Nov 2014	Cold-wet
		Plot 4	15°39′20 N; 92°48′58	2,104	92	426	13.8	76.3	a, h, k	Apr 2015	Dry
		Plot 5	15°39′31 N; 92°48′59	2,050	75	12	19.2	73.3	a, e, m	Jul 2015	Warm-wet
		Plot 6	15°39′28 N; 92°48′57	2,068	93	204	15.29	99.72	a, f, k, n	Jan 2016	Cold-wet
		Plot 7	15°39′24 N; 92°48′52	2,062	89	315	15.2	86	f, k	Feb 2014	Dry
		Plot 8	15°39′33 N; 92°48′54	2,038	85	200	17	90	a, k	May 2014	Warm-wet
		Plot 9	15°39′27 N; 92°48′59	2,077	90	10	13.2	89	a, k	Nov 2014	Cold-wet
		Plot 10	15°39′24 N; 92°48′57	2,088	95	252	14.8	79.1	a, e	Apr 2015	Dry
		Plot 11	15°39′31 N; 92°48′52	2,041	80	289	18.9	80.8	a, e k, h,	Jul 2015	Warm-wet
		Plot 12	15°39′26 N; 92°48′50	2,045	88	125	14.3	97.5	a	Jan 2016	Cold-wet
	TCZ-2	Plot 13	15°39′44 N; 92°48′35	2,098	87	667	16.85	83	f, k	Feb 2014	Dry
		Plot 14	15°39′43 N; 92°48′28	2,091	89	524	17.53	94.3	a, k, d	May 2014	Warm-wet
		Plot 15	15°39′46 N; 92°48′19	2,119	89	802	13.65	73	k	Nov 2014	Cold-wet
		Plot 16	15°39′46 N; 92°48′46	2,087	90	432	15.45	85	0	Apr 2015	Dry

Supplementary Table 1 continued. Sites, coordinates, environmental conditions, species registered, month, year, and season of sample for all 96 plots sampled in El Triunfo Biological Reserve. Species names correspond to a (*C. matudai*), b (*C. stuarti*), c (*Pl. lacertosa*), d (*Pl. hartwegii*), e (*Pl. matudai*), f (*Pl. sagorum*), g (*D. schmidtorum*), h (*Pt. euthysanota*), i (*E. sumichrasti*), j (*L. maculatus*), k (*B. franklini*), l (*B. occidentalis*), m (*B. flavimembris*), and n (*D. xolocalcae*).

Site			Coordinates	Altitude	Canopy cover	Distance to stream	Temperature	Humidity	Species	Month sample	Season
El Triunfo CZ	TCZ-2	Plot 17	15°39′463N; 92°48′41	2,080	94	338	12.6	85.2	k	Jul 2015	Warm-wet
		Plot 18	15°39′44 N; 92°48′23	2,120	95	658	15.4	98.9	e, k	Jan 2016	Cold-wet
		Plot 19	15°39′40 N; 92°48′37	2,065	90	283	17.2	87.6	0	Feb 2014	Dry
		Plot 20	15°39′40 N; 92°48′32	2,065	88	376	15.9	96.7	k	May 2014	Warm-wet
		Plot 21	15°39′48 N; 92°48′31	2,129	95	580	12.89	78.5	0	Nov 2014	Cold-wet
		Plot 22	15°39′51 N; 92°48′37	2,158	89	600	16.45	88	a, k	Apr 2015	Dry
		Plot 23	15°39′48 N; 92°48′37	2,134	92	526	13.5	87.4	a, k	Jul 2015	Warm-wet
		Plot 24	15°39′38 N; 92°48′34	2,054	88	546	13.1	97.1	0	Jan 2016	Cold-wet
		Plot 25	15°39′27 N; 92°48′14	1,981	92	12	15.7	80.1	0	Feb 2014	Dry
		Plot 26	15°39′34 N; 92°48′16	1,973	94	253	19.29	92.9	a, d, e, g, h, f	May 2014	Warm-wet
		Plot 27	15°39′22 N; 92°48′11	1,993	93	133	19.4	79	a, c	Nov 2014	Cold-wet
		Plot 28	15°39′33 N; 92°48′00	1,989	91	395	16.1	84.3	0	Apr 2015	Dry
	TCZ-3	Plot 29	15°39′30 N; 92°48′07	2,008	94	178	20.88	71.2	a, e	Jul 2015	Warm-wet
		Plot 30	15°39′28 N; 92°48′10	2,011	95	167	15.82	89.8	a, k	Jan 2016	Cold-wet
		Plot 31	15°39′23 N; 92°48′04	2,016	94	270	17.2	80	0	Feb 2014	Dry
		Plot 32	15°39′29 N; 92°48′00	2,047	89	50	18.5	95.2	k	May 2014	Warm-wet
		Plot 33	15°39′24 N; 92°47′59	2,045	88	15	16.8	83.4	a, k	Nov 2014	Cold-wet

Supplementary Table 1 continued. Sites, coordinates, environmental conditions, species registered, month, year, and season of sample for all 96 plots sampled in El Triunfo Biological Reserve. Species names correspond to a (*C. matudai*), b (*C. stuarti*), c (*Pl. lacertosa*), d (*Pl. hartwegii*), e (*Pl. matudai*), f (*Pl. sagorum*), g (*D. schmidtorum*), h (*Pt. euthysanota*), i (*E. sumichrasti*), j (*L. maculatus*), k (*B. franklini*), l (*B. occidentalis*), m (*B. flavimembris*), and n (*D. xolocalcae*).

Site			Coordinates	Altitude	Canopy cover	Distance to stream	Temperature	Humidity	Species	Month sample	Season
El Triunfo CZ	TCZ-3	Plot 34	15°39′22 N; 92°48′17	1,997	95	89	17.5	79.8	0	Apr 2015	Dry
		Plot 35	15°39′28 N; 92°48′22	2,016	94	345	19.2	83.4	a	Jul 2015	Warm-wet
		Plot 36	15°39′36 N; 92°48′07	1,928	91	143	12.9	93.4	k, e	Jan 2016	Cold-wet
		Plot 37	15°39′17 N; 92°48′27	1,999	88	53	15.2	86	e	Feb 2014	Dry
		Plot 38	15°39′20 N; 92°48′30	1,995	95	172	19.4	81	k	May 2014	Warm-wet
		Plot 39	15°39′11 N; 92°48′38	2,050	93	249	12.3	91.2	a, e,k	Nov 2014	Cold-wet
		Plot 40	15°38′59 N; 92°48′44	2,110	79	603	16	84	k	Apr 2015	Dry
	TCZ-4	Plot 41	15°39′17 N; 92°48′31	2,073	89	165	16.5	77	k	Jul 2015	Warm-wet
		Plot 42	15°39′12 N; 92°48′30	2,000	90	77	16.45	95.5	a, k	Jan 2016	Cold-wet
		Plot 43	15°39′13 N; 92°48′36	2,029	91	139	16.8	89.4	a	Feb 2014	Dry
		Plot 44	15°39′06 N; 92°48′34	2,034	89	323	18.9	86.7	0	May 2014	Warm-wet
		Plot 45	15°39′14 N; 92°48′33	2,017	96	153	13.1	94	k	Nov 2014	Cold-wet
		Plot 46	15°39′03 N; 92°48′42	2,074	87	508	17.3	87.6	a, k	Apr 2015	Dry
		Plot 47	15°39′08 N; 92°48′36	2,043	92	260	15.8	82.8	a	Jul 2015	Warm-wet
		Plot 48	15°39′06 N; 92°48′46	2,091	91	491	14.8	90.1	0	Jan 2016	Cold-wet
El Quetzal CZ	QCZ-1	Plot 1	15°43′33 N; -92°55′56	2,152	92	10	19.36	75.6	a	Feb 2014	Dry
		Plot 2	15°43′33 N; -9255′58	2,017	92	127	17.47	89	a	May 2014	Warm-wet

Supplementary Table 1 continued. Sites, coordinates, environmental conditions, species registered, month, year, and season of sample for all 96 plots sampled in El Triunfo Biological Reserve. Species names correspond to a (*C. matudai*), b (*C. stuarti*), c (*Pl. lacertosa*), d (*Pl. hartwegii*), e (*Pl. matudai*), f (*Pl. sagorum*), g (*D. schmidtorum*), h (*Pt. euthysanota*), i (*E. sumichrasti*), j (*L. maculatus*), k (*B. franklini*), l (*B. occidentalis*), m (*B. flavimembris*), and n (*D. xolocalcae*).

Site			Coordinates	Altitude	Canopy cover	Distance to stream	Temperature	Humidity	Species	Month sample	Season
El Quetzal CZ	QCZ-1	Plot 3	15°43′35 N; -92°55′53	2,218	94	389	15.9	97	a, k	Nov 2014	Cold-wet
		Plot 4	15°43′37 N; 92°55′50	2,269	90	200	19	73	0	Apr 2015	Dry
		Plot 5	15°43′33 N; 92°55′54	2,182	89	55	16.25	82	k, n	Jul 2015	Warm-wet
		Plot 6	15°43′25 N; 92°55′59	2,080	83	70	17.6	97	k	Jan 2016	Cold-wet
		Plot 7	15°43′29 N; 92°55′53	2,203	91	86	19.24	76	0	Feb 2014	Dry
		Plot 8	15°43′30 N; 92°55′56	2,161	93	154	16.99	87	f, n	May 2014	Warm-wet
		Plot 9	15°43′29 N; 92°56′04	2,030	92	51	15.8	90	0	Nov 2014	Cold-wet
		Plot 10	15°43′29 N; 92°56′02	2,057	90	167	18.9	74	k	Apr 2015	Dry
		Plot 11	15°43′37 N; 92°55′55	2,167	94	183	16.34	85	a, k	Jul 2015	Warm-wet
		Plot 12	15°43,39 N; 92°55′52	2,229	95	48	17	92	0	Jan 2016	Cold-wet
		Plot 13	15°42′58 N; 92°56′15	1,693	83	43	15.4	78	e	Feb 2014	Dry
		Plot 14	15°42′57 N; 92°56′20	1,652	80	12	20.76	76.5	a, j, e	May 2014	Warm-wet
		Plot 15	15°42′54 N; 92°56′22	1,649	84	0	16.35	85	a, e	Nov 2014	Cold-wet
	QCZ-2	Plot 16	15°43′00 N; 92°56′18	1,677	89	0	22.179	77.5	a, e	Apr 2015	Dry
		Plot 17	15°42′58 N; 92°56′24	1,662	76	3	19.3	88.1	l, e	Jul 2015	Warm-wet
		Plot 18	15°42′52 N; 92°56′25	1,621	85	0	18.38	90.88	l, a, e, h	Jan 2016	Cold-wet
		Plot 19	15°43′01 N; 92°56′17	1,685	81	0	16.4	79	0	Feb 2014	Dry

Supplementary Table 1 continued. Sites, coordinates, environmental conditions, species registered, month, year, and season of sample for all 96 plots sampled in El Triunfo Biological Reserve. Species names correspond to a (*C. matudai*), b (*C. stuarti*), c (*Pl. lacertosa*), d (*Pl. hartwegii*), e (*Pl. matudai*), f (*Pl. sagorum*), g (*D. schmidtorum*), h (*Pt. euthysanota*), i (*E. sumichrasti*), j (*L. maculatus*), k (*B. franklini*), l (*B. occidentalis*), m (*B. flavimembris*), and n (*D. xolocalcae*).

Site			Coordinates	Altitude	Canopy cover	Distance to stream	Temperature	Humidity	Species	Month sample	Season
El Quetzal CZ	QCZ-2	Plot 20	15°43′01 N; 92°56′14	1,710	81	25	19.9	78.2	a, e	May 2014	Warm-wet
		Plot 21	15°42′56 N; 92°56′18	1,688	86	0	15.9	86.4	l	Nov 2014	Cold-wet
		Plot 22	15°42′54 N; 92°56′19	1,681	80	9	22.1	77.2	e, l	Apr 2015	Dry
		Plot 23	15°43′00 N; 92°56′13	1,715	78	21	19.5	90.1	a	Jul 2015	Warm-wet
		Plot 24	15°42′59 N; 92°56′12	1,722	76	0	20.4	70.6	0	Jan 2016	Cold-wet
		Plot 25	15°43′00 N; 92°56′34	1,716	70	610	19.7	60	a	Feb 2014	Dry
		Plot 26	15°42′58 N; 92°56′38	1,688	75	650	22.83	79.5	a, b, l	May 2014	Warm-wet
	QCZ-3	Plot 27	15°43′02 N; 92°56′36	1,703	94	483	15.32	82.4	a, f, l	Nov 2014	Cold-wet
		Plot 28	15°42′57 N; 92°56′42	1,679	95	648	14.1	75.2	l, a	Apr 2015	Dry
		Plot 29	15°43′03 N; 92°56′33	1,730	93	534	21.87	74.7	b, e, l	Jul 2015	Warm-wet
		Plot 30	15°42′58 N; 92°56′41	1,695	75	485	21.7	66.3	l	Jan 2016	Cold-wet
		Plot 31	15°42′58 N; 92°56′48	1,647	75	493	19.1	72	a	Feb 2014	Dry
		Plot 32	15°43′02 N; 92°56′45	1,649	73	244	22.2	77	a, l, b	May 2014	Warm-wet
		Plot 33	15°43′02 N; 92°56′41	1,674	94	349	15.3	85	0	Nov 2014	Cold-wet
		Plot 34	15°43′01 N; 92°56′43	1,674	87	314	16.8	78	b, l	Apr 2015	Dry
		Plot 35	15°42′59 N; 92°56′43	1,689	89	406	22.9	72	a	Jul 2015	Warm-wet
		Plot 36	15°42′58 N; 92°56′45	1,674	90	400	20	70	0	Jan 2016	Cold-wet

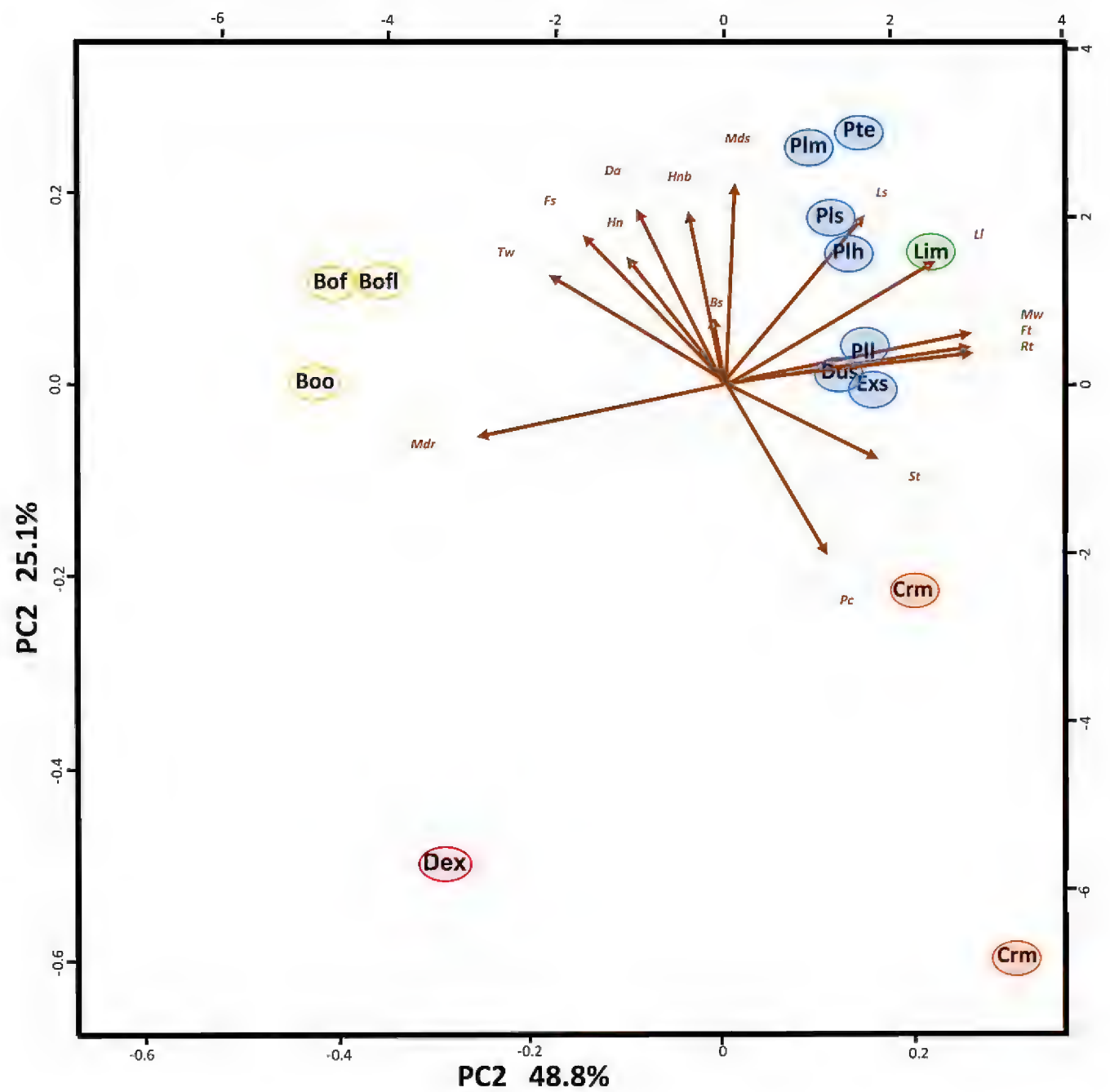
Supplementary Table 1 continued. Sites, coordinates, environmental conditions, species registered, month, year, and season of sample for all 96 plots sampled in El Triunfo Biological Reserve. Species names correspond to a (*C. matudai*), b (*C. stuarti*), c (*Pl. lacertosa*), d (*Pl. hartwegii*), e (*Pl. matudai*), f (*Pl. sagorum*), g (*D. schmidtorum*), h (*Pt. euthysanota*), i (*E. sumichrasti*), j (*L. maculatus*), k (*B. franklini*), l (*B. occidentalis*), m (*B. flavimembris*), and n (*D. xolocalcae*).

Site			Coordinates	Altitude	Canopy cover	Distance to stream	Temperature	Humidity	Species	Month sample	Season
El Quetzal CZ	QCZ-4	Plot 37	15°43,20 N; 92°56′34	1,789	70	437	20.25	70	0	Feb 2014	Dry
		Plot 38	15°43′17 N; 92°56′32	1,783	75	561	17.9	85	0	May 2014	Warm-wet
		Plot 39	15°43′17 N; 92°56′33	1,783	86	548	14.2	83	l	Nov 2014	Cold-wet
		Plot 40	15°43′26 N; 92°56′24	1,799	85	565	15.73	84.5	l	Apr 2015	Dry
		Plot 41	15°43′19 N; 92°56′24	1,852	78	485	22.78	74.6	a, l	Jul 2015	Warm-wet
		Plot 42	15°43′20 N; 92°56′30	1,814	75	591	20.72	83.76	a	Jan 2016	Cold-wet
		Plot 43	15°43′24 N; 92°56′27	1,777	80	621	21.8	70	l	Feb 2014	Dry
		Plot 44	15°43′24 N; 92°56′22	1,848	76	488	17.5	88	a	May 2014	Warm-wet
		Plot 45	15°43′24 N; 92°56′31	1,754	77	629	15.8	80	0	Nov 2014	Cold-wet
		Plot 46	15°43′17 N; 92°56′28	1,816	82	433	17	75	0	Apr 2015	Dry
		Plot 47	15°43′23 N; 92°56′25	1,831	72	501	20.7	76	a, l	Jul 2015	Warm-wet
		Plot 48	15°43′23 N; 92°56′22	1,862	86	638	17.8	83	0	Jan 2016	Cold-wet

Supplementary Table 2. Functional Traits Matrix used to determine functional groups among amphibian species; in parenthesis is the species code for the PCA of the functional group figure on the next page (Supplementary Fig 1). Species names correspond to: Crm (*C. matudai*), Crs (*C. stuarti*), Pll (*Pl. lacertosa*), Plh (*Pl. hartwegii*), Plm (*Pl. matudai*), Pls (*Pl. sagorum*), Dus (*D. schmidtorum*), Pte (*Pt. euthysanota*), Exs (*E. sumichrasti*), Lim (*L. maculatus*), Bof (*B. franklini*), Boo (*B. occidentalis*), Bofl (*B. flavimembris*), and Dex (*D. xolocalcae*).

The descriptions of trait column headers and associated values are as follows: **Bs** (body size): S, Small (20–40 mm); M, Medium (41–61 mm); L, Large (61–80 mm); EL, Extra-large, (> 81 mm). **Tw** (toe webbing): Abs, Absent; Bas, Basal; Mod, Moderate; Ext, Extended. **Mw** (mouth width in proportion to SVL): S, Small (<20%); M, Medium (21–30%); L, Large (> 30%). **Ll** (leg length in proportion to SVL): S, Small (< 1–35% of SLV); M, Medium (36–80%); L, large (81–130%); EL, Extra-Large (> 130%). **St** (dorsum skin thickness/type): 1 = thin/smooth; 2 = thin/granular; 3 = thin/granular-tuberculated; 4 = thin/smooth-granular; 5 = thick/postulated; 6 = thick/smooth to tuberculated; 7 = thick/tuberculated; 8 = thick/pustulated; 9 = thin/tuberculated; 10 = thin/scale. **Rt** (respiration type): Lung, predominantly pulmonary; Skin, predominantly cutaneous. **Ft** (fertilization type): Int, internal; Ext: external. **Mdr** (male reproductive display for female response): Ac, acoustic; Hor, hormonal. **Mds** (male reproductive display site) and **Fs** (fertilization site): UndWb, Understory above waterbody; InWb; In waterbody; Ter, Terrestrial; TerNxWb, Terrestrial next to waterbody, Fos, Forsorial; ArbUnd, Arboreal or understory; TerUnd, Terrestrial or understory. **Ls** (Laying site): TerDirDev, Terrestrial with direct development; Viv, viviparous; TreeWbTad, Tree waterbody tadpoles; TerWbTad, Terrestrial waterbody tadpoles; UndWbTad, Understory waterbody tadpoles; FoamWbTad, Foam nest waterbody tadpoles. **Pc** (clutch parental care): Pres = Present; Abs = Absent. **Da** (daily activity): Noc = nocturnal; Cath = cathemeral. **Hnb** (basic habitat in non-breeding season): Arb = arboreal; Fos = fossorial; Und = understory; Ter = terrestrial; TerUnd = terrestrial/understory; Und/arb = understory/arboreal; TerWb = terrestrial next to water bodies. **Hn** (Numbers of habitats used during the non-breeding season).

Functional group	Species	Bs	Tw	Mw	Ll	St	Rt	Ft	Mdr	Mds	Fs	Ls	Pc	Da	Hnb	Hn
5	Bof	L	Mod	M	S	1	skin	Int	Hor	TerUnd	TerUnd	TerDirDev	Abs	Noc	TerUnd	3
5	Boc	S	Mod	M	ExS	1	skin	Int	Hor	TerUnd	TerUnd	TerDirDev	Abs	Noc	TerUnd	3
5	Bofl	L	Mod	M	S	1	skin	Int	Hor	TerUnd	TerUnd	TerDirDev	Abs	Noc	TerUnd	3
4	Dex	S	Mod	M	ExS	1	skin	Int	Hor	Arb	Arb	TerDirDev	Abs	Noc	Arb	1
2	Crm	M	Bas	L	M	5	lung	Ext	Ac	Ter	Ter	TerDirDev	Pres	Cath	Ter	1
2	Crs	S	Bas	L	M	3	lung	Ext	Ac	TerUnd	Ter	TerDirDev	Pres	Noc	UndArb	3
3	Dus	S	Sem	L	L	1	lung	Ext	Ac	UndWb	InWb	TerWbTad	Abs	Noc	UndArb	2
3	Exs	S	Sem	L	L	2	lung	Ext	Ac	UndWb	InWb	TerWbTad	Abs	Noc	UndArb	2
3	Plh	L	Sem	L	L	2	lung	Ext	Ac	ArbUndWb	InWb	TerWbTad	Abs	Noc	UndArb	2
3	Pll	M	Sem	L	L	2	lung	Ext	Ac	UndWb	InWb	TerWbTad	Abs	Noc	UndArb	2
3	Plm	M	Sem	L	L	2	lung	Ext	Ac	TerrUndWb	InWb	TerWbTad	Abs	Noc	TerUnd	3
3	Pls	M	Sem	L	L	2	lung	Ext	Ac	ArbUndWb	InWb	TerWbTad	Abs	Noc	UndArb	3
3	Pte	S	Sem	L	L	1	lung	Ext	Ac	TerrUndWb	UndWb	UndWbTad	Abs	Noc	UndArb	2
1	Lim	EL	Ext	L	ExL	6	lung	Ext	Ac	InWb	InWb	TerWbTad	Abs	Noc	Terwb	1



Supplementary Figure 1. Principal Component Analysis, grouping the five sites present in the core zones according to the functional traits. Species names correspond to Crm (*C. matudai*), Crs (*C. stuarti*), Pll (*Pl. lacertosa*), Plh (*Pl. hartwegii*), Plm (*Pl. matudai*), Pls (*Pl. sagorum*), Dus (*D. schmidtorum*), Pte (*Pt. euthysanota*), Exs (*E. sumichrasti*), Lim (*L. maculatus*), Bof (*B. franklini*), Boo (*B. occidentalis*), Bofl (*B. flavimembris*), and Dex (*D. xolocalcae*)